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Relationships of the Extinct Rodent *Cricetops* to *Lophiomys* and the Cricetinae (Rodentia, Cricetidae)

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ABSTRACT

Cricetops, an extinct cricetid from the mid-Oligocene of Mongolia and Kazakhstan, and *Lophiomys,* a peculiar cricetid living in eastern Africa, share dorsoventral expansion of the jugal bone and enclosure of fossettids in the transverse crests of M_1. They are proposed as each other's closest relative and included in the subfamily Lophiomyinae. Emphasis on transverse wear is shared by these genera and the living Cricetinae: *Cricetulus, Phodopus, Mesocricetus,* and *Cricetus.* The two subfamilies are considered closest relatives and placed in the muroid family Cricetidae. *Cricetops* and the living cricetines are chiefly northern Asiatic groups. Immigration to Africa from Asia is proposed for the ancestors of *Lophiomys.*

INTRODUCTION

The molar teeth of *Cricetops dormitor,* an Oligocene cricetid rodent from Asia, are striking for their lophodont design and transverse wear facets. The primary lingual and buccal cusps are opposite one another and form transverse ridges that stand in high relief from the intervening valleys. A remarkably similar condition occurs in the living African cricetid *Lophiomys*; Schaub (1925) was struck by the likeness of the crown pattern of M^1 to that of lophodont mastodonts; the same likeness is obvious in *Cricetops.*

The relationships of *Cricetops* and *Lophiomys* to cricetids are uncertain. The three recognized species of *Cricetops* are now known from both Mongolia and Kazakhstan. *Cricetops dormitor* was described and figured by Matthew and Granger (1923); the generic name selected indicates the similarity of the teeth in proportions and patterns to those of

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Cricetus. The primitive structure of the zygomatic arch in *Cricetops,* however, led the authors to speculate on relationships but not to place the genus definitely in a classification. Their illustration of the dentition (*ibid.,* fig. 4) gives little sense of either topography or wear, and the tooth proportions are distorted. A lateral view of the skull (*ibid.,* fig. 1) conveys the significant topographic information about the teeth.

Several notable contributions have been made to the description of *Cricetops.* Schaub (1925) described in detail and accurately illustrated occlusal views of the dentition in a specimen of *C. dormitor* donated by Matthew to the Naturhistorisches Museum in Basel. Argyropulo (1938) described *C. affinis.* Shevyreva (1965) added two species, *C. aeneus* and *C. elephantulus,* and made *C. affinis* a synonym of *C. dormitor.* Original descriptions and figures of dentitions appear in papers by Shevyreva (*ibid.*) and Kowalski (1974); those of skulls and mandibles in Shevyreva (1965), Vorontsov (1979), Repenning (1968), and Lindsay (1977). Vorontsov (1982, fig. 59) restored the masticatory musculature of *C. aeneus.*

Matthew and Granger (1923) tentatively associated *Cricetops* and *Selenomys,* a rodent from the same horizon, in the family Cricetopidae but did not associate it with any particular taxon in the Myomorpha. Schaub (1925) on the basis of dental evidence assigned *Cricetops* to the Cricetidae and suggested closer relationship to *Eumys* and the New World Hesperomyinae than to the Old World Cricetodontinae. Simpson (1945) placed the genus with *Selenomys* and *Kanisamys* in a new tribe Cricetopini of the subfamily Cricetinae. Schaub (1958) restricted this tribe to *Cricetops.* Mellett (1968) suggested that *Selenomys* might be an aplodontid. Black (1972) transferred *Kanisamys* to the Rhizomyidae.

Lophiomys, a monotypic genus, occurs in Somalia, Ethiopia, Sudan, Kenya, Uganda, and Tanzania; a subfossil specimen was found in Israel (Dor, 1966). The taxonomic history of *Lophiomys* is given by Ellerman (1940); morphology and behavior are described by Milne Edwards (1867b), Ellerman (1940), and Kingdon (1974).

Milne Edwards (1867a and 1867b) named and described *Lophiomys imhausii.* He pointed out the similarities of the molar teeth to those of *Cricetus* and similarities of the skull, disregarding specialization of the temporal vault, to the design in murids. However, he did not place *Lophiomys* in the Muridae but created a family of equal rank, the Lophiomyidae, to receive it. This decision was based on the unique combination of characters that occur in the genus: expanded temporal vault, rudimentary clavicles, bushy tail, and unusual structure of the stomach and its annexes.

Tullberg (1899), Ellerman (1940), and Vorontsov (1979) followed Milne Edwards in assigning *Lophiomys* to a family of its own, equal in rank to the Muridae. Other authors, however, gave greater weight to the similarity of the dentition to that of hamsters. Winge (1941) united the genus with the Old World taxa *Cricetus, Calomyscus,* and *Myospalax* in a taxon within the Cricetidae. Schaub (1925) considered *Lophiomys* to belong with other cricetids. He concluded that the teeth exhibit a new evolutionary tendency in which cusps begin to fuse into transverse lophs, and that the genus could not be placed in a taxon with *Cricetulus, Cricetus,* and *Mesocricetus.* Simpson (1945) placed *Lophiomys* by itself in the Lophiomyinae, a subfamily of the Cricetidae. Stehlin and Schaub (1950) listed the tribes Cricetini and Lophiomyini as the only two taxa included in the subfamily Cricetinae. Lavocat (1973) included the Lophiomyinae in the Nesomyidae; he suggested that this family contained the descendants of the extinct Afrocricetodontinae. Lavocat derived the Cricetinae from the extinct Eurasian Cricetodontinae. Fossil evidence for this hypothesis has been presented in detail by Fahlbusch (1972).

The striking similarity of the dentitions of *Cricetops* and *Lophiomys* has gone unnoticed. Published figures described the morphology of the teeth incompletely, and the relief of the cusps and the position and attitude of wear facets were omitted. I present new descriptions and figures that remedy the situation. The implied hypotheses of relationship and parallelism are investigated. Redescription of the skull of *Cricetops* is postponed for consideration with other Oligocene cricetids.

ACKNOWLEDGMENTS

The unusual molar crown morphology of *Cricetops* was called to my attention by Miss Marie A. Lawrence. I appreciate the benefit of many discussions with her and with Drs. Karl Koopman and Guy Musser on selection of a comparative sample and on presentation and interpretation of the results. Ms Lorraine Meeker and Mr. Chester Tarka guided me in the process of illustration. Ms Joan Whelan took the scanning electron micrographs. The quality of the manuscript has been enhanced by the careful criticism of Drs. Michael D. Carleton and Karl F. Koopman.

I thank the Committee on Released Time and Prof. Martin Stevens, Dean of the School of Liberal Arts and Sciences, Baruch College, who granted me a reduced teaching schedule so that I might carry out this research. Facilities, specimens, and equipment were made available to me by the departments of Vertebrate Paleontology and of Mammalogy at the American Museum of Natural History.

NOMENCLATURE OF MOLAR CROWN MORPHOLOGY

Current nomenclature for rodent tooth morphology is based primarily on the descriptions given by Wood and Wilson (1936). These names of the major cusps are in accord with those applied by Schaub (1925) to the cricetid dentition and with the embryologic evidence presented by Gaunt (1961) for *Mesocricetus*. The names applied to other structures, the lophs and lesser cusps, have been accepted widely among paleontologists. Reig (1977) proposed a nomenclature for cricetid molars that changes some of the terms and creates usages special to the group.

Reig (*ibid.*) perpetuated a misnomer for the longitudinal crests in cricetid molars. In the upper molars this feature connects the protocone and hypocone and in lowers, the protoconid and hypoconid. Schaub and other German paleontologists have named this crest the Längsgrat. Wood and Wilson (1936) called the structure the mure in upper molars and the ectolophid in lowers. Hooper (1957) applied mure to the longitudinal crests in both upper and lower molars and applied ectolophid to a buccal extension of the mesolophid, a transverse crest; he called the reflection of this feature in upper molars the entoloph. Hershkovitz (1962) followed Hooper in usage of ectolophid, but called its reflection in upper molars the enteroloph.

Reig (1977) adopted the novel designations of Hershkovitz and rejected the original terms that are currently used by paleontologists. He added the suffix -id to mure in lower molars and proposed the name murid. The confusion that arises when a morphological feature and a taxon have the same name is well illustrated by the term hystricomorph and is best avoided.

Rather than perpetuate an atypical use of terms for cricetid molars, I propose a return to traditional nomenclature as it has been adapted to cricetid teeth by Mein and Freudenthal (1971). The longitudinal crest connecting lingual cusps, protocone and hypocone, of upper molars is termed the entoloph rather than mure; this expresses its nature as the reflection of the ectolophid, which connects the primary buccal cusps of the lower molars. The minor transverse crests opposite the mesoloph and mesolophid are termed entomesoloph in upper molars and ectomesolophid in lowers.

Although I agree with Reig that the hypolophid in lower molars is more closely associated with the entoconid than the hypoconid, to change its name would create unnecessary confusion.

MEASUREMENTS

Dimensions of the molars were measured to the nearest 0.1 mm. on the mechanical stage of a stereomicroscope in the Department of Mammalogy. The dentition was oriented so that the vertical cross hair longitudinally bisected the entire tooth row. The length of each tooth was measured between points on this line. Widths were measured perpendicular to the bisecting line.

Measurements and comparisons were made for the purpose of exploration rather than for rigorous taxonomic scrutiny. The dentitions of some genera were so small compared with others that error in measurement was proportionally very great.

SPECIMENS EXAMINED

All specimens are in collections at the American Museum of Natural History

(AMNH). Recent taxa are housed in the Department of Mammalogy, *Cricetops* and *Eumys* in the Department of Vertebrate Paleontology; some specimens of *Eumys* are part of the Frick Collection (F:AM).

Cricetops dormitor. Upper dentitions: AMNH 19046, 19051, 21660, 81202, 85325, 85327, 85330, 85340, Loh campsite; AMNH 19049, 19054 (holotype), 19055, 84179, 84371, Grand Canyon, 10 mi. W of Loh. Lower dentitions: AMNH 81398, 82141, Loh campsite; AMNH 19054 (holotype), 81429, 82047–82348, 83968, 84180, 84387, 84439, Grand Canyon, 10 mi. W of Loh; AMNH 19043, 81242, 12 mi. E of Loh; AMNH 82318, 2 mi. SW of Loh. *Cricetops* cf. *aeneus.* Lower dentition: AMNH 101534 (cast), Tatal Gol (=Grand Canyon). All specimens are from the Hsanda Gol Formation, middle Oligocene age, Tsagan Nor Basin, Outer Mongolia.

Lophiomys imhausii. AMNH 33331–33333, Laikipia Escarpment, Kenya; AMNH 54008, Harrar Prov., Ethiopia; AMNH 55881–55882, Nyeri, Kenya; AMNH 80969 (not measured), N Aberdare Mts., Kenya; AMNH 80970, SW Kenya; AMNH 80971 (neonate; not used for measurement), Kenya; AMNH 146561, 147455, zoo specimens from Africa; AMNH 187455, 187457, 187458, S Laikipia Forest, Nyeri, Kenya.

Cricetus cricetus. AMNH 3013, Hungary; AMNH 87106, Lepinsk, Kazakh S.S.R.; AMNH 176479–176483, Wörrstadt, bei Alzey, West Germany.

Mesocricetus auratus. AMNH 144768–144769, 144771, 144955–144956, 150013–150014, 185293–185294, 185317, laboratory and zoo specimens.

Cricetulus barabensis. AMNH 57896, Sain Noin Khan, Outer Mongolia; AMNH 84108, Orok Nor, Outer Mongolia; AMNH 178809, Srentensk, Chita Dist., U.S.S.R. *C. longicaudatus.* AMNH 57722–57723, Artsa Bogdo, Outer Mongolia. *Cricetulus migratorius.* AMNH 57832, Gun Burte, Outer Mongolia; AMNH 57834, Tsagan Nor, Outer Mongolia; AMNH 88831–88832, Dasht, Khorassan, Iran; AMNH 171190, Khurramabad, Lurestan, Iran. *Cricetulus triton.* AMNH 34073, Nojido, Korea; AMNH 56392, base of Taipei Shan, Ch'in Ling Mts., Shensi, China.

Phodopus sungorus. AMNH 46397–46399, 140 mi. SE of Ulan Bator, Outer Mongolia; AMNH 57897–57898, Uskuk, Outer Mongolia; AMNH 57908, Tuerin, Outer Mongolia; AMNH 57915, 30 mi. NE of Tsetsen Wang, and AMNH 57918, 40 mi. SW of Tsetsen Wang, Outer Mongolia; AMNH 84028, Jichi Ola, Outer Mongolia. *P. roberovskii.* AMNH 37839, Yu-ling-fu, Shensi, China.

Calomyscus bailwardi. AMNH 88839, 88841–88842, Dergermatie, Kurkhud Mts., Khorassan, Iran; AMNH 171192, 171199–171200, Khurramabad, Lurestan, Iran; AMNH 212079, 212081, 212084–212085, SE slope Mt. Chiltan, *ca.* 15 mi. SW Quetta, Quetta-Pishin Dist., West Pakistan.

Eumys. Upper dentitions: *Eumys elegans.* AMNH 94102, 94108, F:AM 94875, 94878, 94931, 103375, White Buttes, Slope Co., N.D.; AMNH 96420, F:AM 94929, Fitterer Ranch, Stark Co., N.D.; F:AM 103376, Reva Gap, Harding Co., S.D.; AMNH 1430, head of Corral Draw, Pennington-Shannon Co. boundary area, S.D.; F:AM 103378, 6 mi. E of Grover, Weld Co., Colo. *Eumys parvidens.* F:AM 94917, White Buttes, Slope Co., N.D. Lower dentitions: *Eumys elegans.* AMNH 94082, 94159, F:AM 94862, 94866, White Buttes, Slope Co., N.D.; F:AM 94959, 95003, 113189, Fitterer Ranch, Stark Co., N. D.; F:AM 94958, Little Badlands, Stark Co., N.D., F:AM 113190, Reva Gap, Harding Co., S.D.; F:AM 103378, 6 mi. E of Grover, Weld Co., Colo.; AMNH 5487, Cedar Creek, Logan Co., Col. *Eumys parvidens.* AMNH 5535, Cedar Creek, Logan Co., Colo. All specimens are from the Brule Formation and equivalents, middle Oligocene (Orellan) age, United States.

DENTITIONS OF *CRICETOPS* AND *LOPHIOMYS*

The teeth of both *Cricetops* and *Lophiomys* are characterized by paired cusps of about equal height that form nearly transverse lophs, which stand in high relief from the intervening troughs (figs. 1 and 2). A continuous wear surface extends from one end of the dentition to the other; it ascends the anterior face of each loph, descends its posterior face, continues across the floor of the trough to the rear, and ascends the next loph.

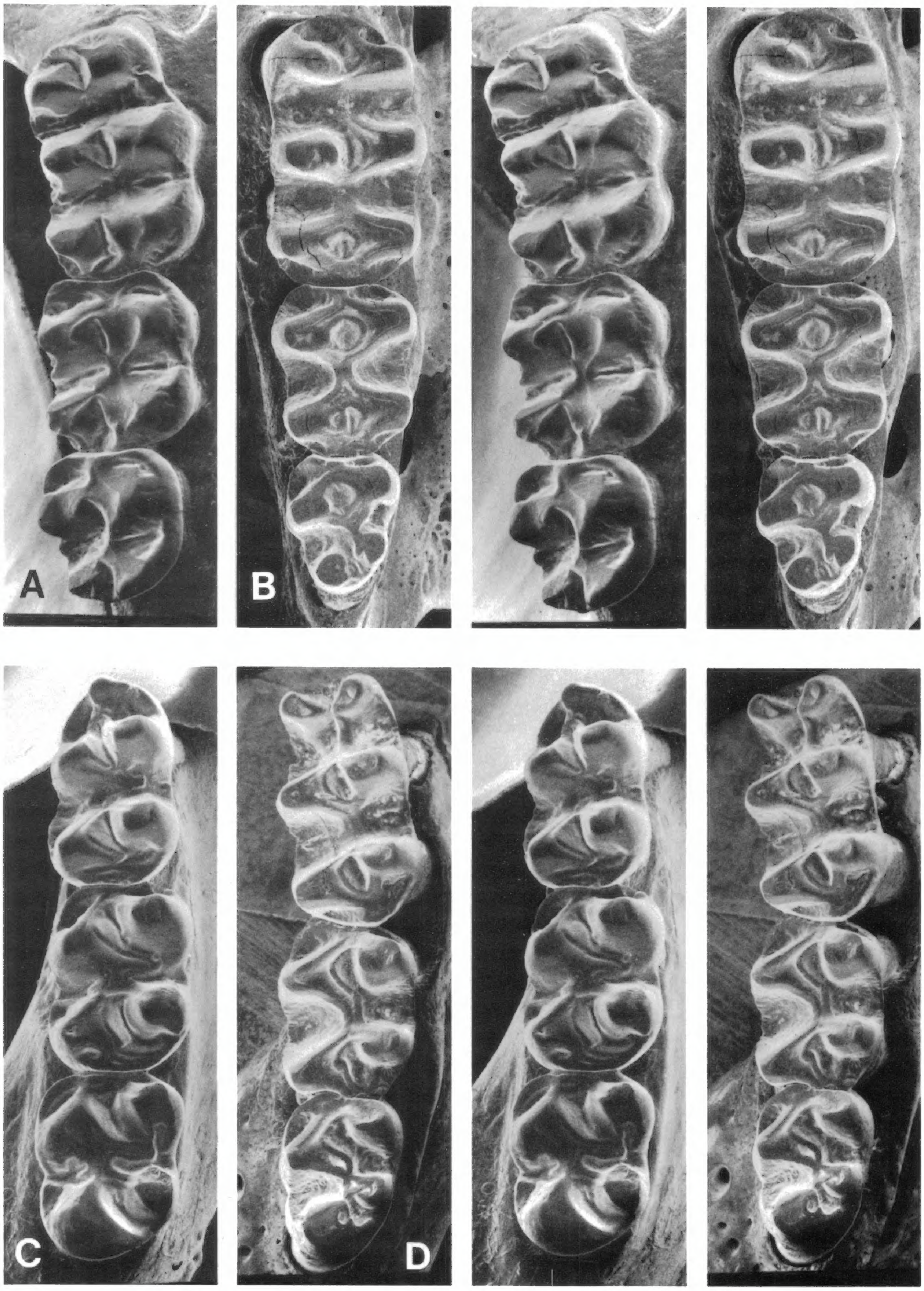

FIG. 1. Stereoscopic scanning electron micrographs of molar toothrows. *Cricetops dormitor* (AMNH 19054, holotype), approx. ×8.1: A, upper right; C, lower right, reversed. *Lophiomys imhausii* (AMNH 147455), approx. ×6.4: B, upper right; D, lower left. Anterior at top, buccal to left.

Dental morphology of both genera suggests that the method of chewing was similar to that described in *Mesocricetus* by Gorniak (1977). Movement of the lower teeth is great-

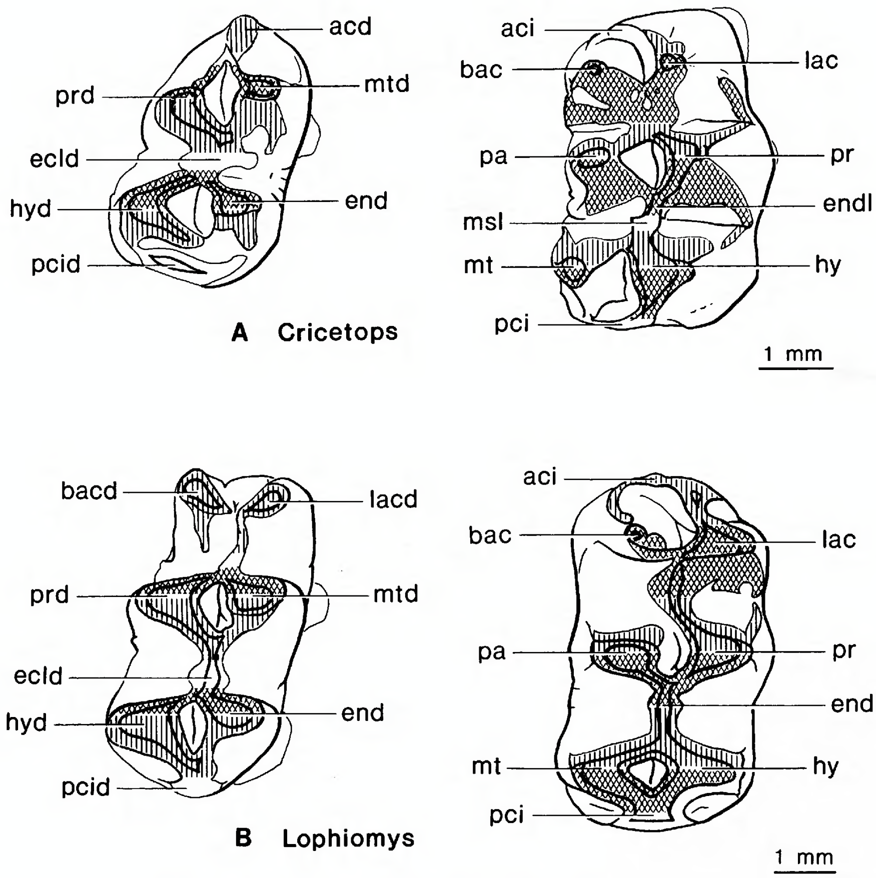

FIG. 2. First molars of A, *Cricetops dormitor* and B, *Lophiomys imhausii* drawn from scanning electron micrographs as lower left (left side of fig.) and upper right (right side of fig.). *Abbreviations:* acd, anteroconid; aci, anterior cingulum; bac, buccal anterocone; bacd, buccal anteroconid; ecld, ectolophid; end, entoconid; endl, endoloph; hy, hypocone; hyd, hypoconid; lac, lingual anterocone; lacd, lingual anteroconid; msl, mesoloph; mt, metacone; mtd, metaconid; pa, paracone; pci, posterior cingulum; pcid, posterior cingulid; pr, protocone; prd, protoconid. Crests in lower teeth close anterior to corresponding crests in uppers; identical patterns indicate opposing wear surfaces in lower and upper teeth. Anterior at top, buccal to left; transverse crests horizontal.

ly restricted by the interlocking ridges and troughs, when the dentitions are manually occluded. The active side of the lower dentition of *Lophiomys* can only be swung medially in an arc across the upper teeth; at the same time the condyle on that side of the jaw pivots and slides anteriorly in an arcuate fossa that is concave medially. The fossa in *Cricetops* looks straighter, but occlusal movement of the teeth appears to be the same. The many transverse striations on the worn surfaces in both genera support this view of occlusion. Apical flattening of the cusps increases with age; the lack of striations on the apexes suggests that this wear is an effect incidental to occlusal direction.

M^1 is characterized by three transverse lophs. The first, the anteroloph, is comprised of buccal and lingual anterocones; the second, the protoloph, of paracone and protocone; the third, the metaloph, of metacone and hypocone. The series of lophs is flanked by low anterior and posterior cingula, which are more fully developed in *Lophiomys.* Between each pair of cusps are basins termed fossettes; their continuity with the deeper, transverse troughs

TABLE 1
Molar Tooth Dimensions

	Cricetops dormitor (N = 13)						*Lophiomys imhausii* (N = 12)					
	Length			Width			Length			Width		
	$\bar{X}$	OR	v	$\bar{X}$	OR	v	$\bar{X}$	OR	v	$\bar{X}$	OR	v
M^1	4.4	4.1–4.9	5.9	2.7	2.5–3.0	6.2	6.0	5.3–6.6	5.3	3.5	3.3–3.9	4.7
M^2	2.9	2.7–3.2	5.1	2.8	2.6–3.0	5.2	3.8	3.2–4.1	6.0	3.4	3.1–3.8	5.3
M^3	2.6	2.4–2.8	5.9	2.5	2.4–2.8	4.6	2.9	2.7–3.3	5.7	2.6	2.4–2.8	4.2
M_1	3.5	3.2–3.8	5.5	2.4	2.1–2.8	8.3	5.2	4.4–5.6	6.3	3.0	2.7–3.4	6.5
M_2	3.1	2.7–3.5	7.8	2.6	2.4–2.9	6.1	3.9	3.6–4.2	4.8	3.2	2.9–3.5	5.0
M_3	3.1	2.7–3.6	9.3	2.6	2.3–3.0	8.5	3.5	3.2–3.7	4.8	2.8	2.6–3.0	4.0

Abbreviations: N, sample size; OR, observed range; v, coefficient of variation; $\bar{X}$, mean.

is broken, because they are elevated with the cusps. A median longitudinal crest, the endoloph, runs across the troughs and joins loph to loph; it is worn low. In *Lophiomys* it is about equally linked anteriorly to protocone and paracone and posteriorly to metacone and hypocone. In *Cricetops* broad exposure of dentine shows that it is joined primarily to the lingual cusps; this association is clearly borne out by the morphology of M^3 in both taxa. The presence of the endoloph shows that the troughs are formed by union of buccal and lingual embayments that are opposite one another. The exposure of dentine in the endoloph broadens in the second trough of the type specimen of *Cricetops dormitor*; in others a thin mesoloph extends almost to the buccal edge of the tooth; *Lophiomys* has no trace of this feature. The fossette in the metaloph is open posteriorly in *Cricetops* and completely enclosed in *Lophiomys*.

M^2 of both taxa repeats the patterns seen in M^1, but only two lophs, protoloph and metaloph, are present; anteroconids are lacking, and the endoloph is not as completely worn down. In *Cricetops* the anterior cingulum is better developed; a narrow mesoloph runs anterolabially from the endoloph just anterior to its junction with the metaloph. As in M^1 the fossette in the metaloph is open posteriorly in *Cricetops* but is completely enclosed in *Lophiomys*. The tooth is nearly square in *Cricetops* and tapers posteriorly in *Lophiomys*.

M^3 differs markedly in the two taxa. In *Cricetops* it resembles M^2. However, the buccal embayment curves anteriorly between paracone and protocone, and its tip is not constricted to form a fossette. The endoloph is strong and clearly connects protocone and hypocone. The hypocone and metacone are opposite one another. The fossette between them is merely a posterior indentation of the crown. The metacone in the illustration of *Cricetops* (fig. 1) has a chip missing from its posterior side. A thin, short mesoloph extends laterally from the anterior side of the metaloph. In *Lophiomys* the anterior cingulum is narrower; the protoloph contains a fossette. The endoloph is strong, but there is no trace of a mesoloph. The hypocone is not opposite but is anteromedial to the metacone and contributes to the triangular shape of this tooth.

Overall differences between the two genera are few in the upper dentitions. In *Cricetops* the cusps and thus the lophs are broader. The buccal cusps, the paracones and metacones, of M^1 and M^2 and the paracone of M^3 appear to be rotated medially in *Cricetops* so that a sulcus is present on the posterolateral side of each; wear creates an abrupt edge at the posterior facet. The troughs in *Cricetops* have a groove in the bottom, whereas the deepest part in *Lophiomys* is a smoothly curved surface.

The upper dentitions of *Cricetops* and *Lophiomys* differ in size and proportions (tables 1, 2, and 3). In *Cricetops* M^1 occupies 45 percent of the tooth row length. The protoloph and metaloph of M^1 and the protoloph of M^2 are approximately equal in width and are the widest parts of the dentition. Even the width of the protoloph of M^3 is about 90

percent of this dimension. M^2 is approximately square, and M^3 is similar but more rounded posteriorly. In *Lophiomys* M^1 is slightly longer and M^3 shorter than in *Cricetops*. The three lophs of M^1 are approximately equal in width and are slightly wider than or equal to the protoloph of M^2. Lophs posterior to this one are progressively narrower, and the entire tooth row tapers. M^3 is roughly triangular.

The lower dentitions of *Cricetops* and *Lophiomys* are constructed on a plan similar to the upper, with transverse lophs separated by troughs and a continuous wear surface over the topography. The lophs are more obliquely oriented to the long axis of the teeth than in the upper molars, although the tooth rows themselves are nearly parallel to the longitudinal axis of the head. During occlusion the lower teeth pass obliquely across the uppers and describe an arc centered on the condyle.

M_1 has three transverse ridges. In *Cricetops* the anterolophid has but one medial cusp, and the anterior ridge is short; in *Lophiomys* buccal and lingual anteroconids are present and form a wide ridge. As wear progresses, fossettids are enclosed between the protoconid and metaconid in the metalophid and between the hypoconid and entoconid in the hypolophid. The posterior cingulum is equally well developed in both genera. The ectolophid, a median longitudinal crest that is analogous to the endoloph, is worn nearly flush with the floor of the transverse troughs. Its connection with the hypoconid is clear in M_3 of *Cricetops*.

M_2 is very similar in the two genera; two transverse lophids are separated by a trough and flanked by cingula. The fossettids in the metalophid and hypolophid are open posteriorly in both genera. The posterior arms of the protoconid and hypoconid extend farther buccally in *Cricetops* and nearly close them off. A tiny mesolophid is present in one fossil specimen, AMNH 81398.

The metalophids in M_3 are similar to the lophids of anterior teeth. The posterior arm of the protoconid is well developed in *Cricetops*; it is farther posterior than in M_2 and could be mistaken for a mesolophid. *Lophiomys* bears no trace of this feature. The hypolophid is developed as a substantial ridge with opposite cusps in *Cricetops*, and a fossettid is enclosed. In *Lophiomys* the hypolophid is narrower than the metalophid; the hypoconid, which is posterobuccal to the entoconid, forms the heel of the molar; the fossettid is open posteriorly.

As in the upper molars, cusps and thus lophids are broader in *Cricetops* than in *Lophiomys*. The lower molars of the two genera differ in size and proportions (tables 1, 2, and 3). In *Cricetops* M_1 is the longest tooth, but it occupies only a little more than one-third of the tooth row length. The metalophid and hypolophid of M_2 and the metalophid of M_3 are of similar width and are the widest parts of the dentition. In *Lophiomys* M_1 occupies a markedly greater percent of tooth row length and M_3 a lesser fraction. The metalophid and hypolophid of M_2 are of equal width and are the widest parts of the dentition. The hypolophid of M_1 is 95 percent as wide. M_3 is narrower than the anterior teeth; the hypolophid is markedly so and gives the tooth an elongated, somewhat triangular shape.

COMPARISONS

I compared the cheek teeth of *Cricetops* and *Lophiomys* with those of rodents that have been considered to be close relatives of *Cricetus*. These are *Cricetus* itself, *Mesocricetus, Cricetulus, Phodopus,* and *Calomyscus*. I also examined *Eumys,* the extinct cricetid common in the Oligocene of North America.

The most interesting aspect of the comparison is the way in which upper and lower molars occlude. In all of these dentitions chewing could only occur on one side or the other at any one time. The dentitions were fitted together manually, and the lower teeth were moved lingually or anterolingually as the interlocking of cusps allowed. Wear facets on the teeth were then examined to determine if there were supporting evidence for the direction of unimpeded gliding.

In *Cricetops* and *Lophiomys* the pairs of cusps, lingual and buccal, form strong, transverse lophs and lophids. Movement of the lower teeth is greatly restricted by the interlocking ridges and troughs.

The teeth of *Cricetus* and *Mesocricetus* (fig. 3A) are very similar to those of *Lophiomys* and *Cricetops*. Paired cusps form strong,

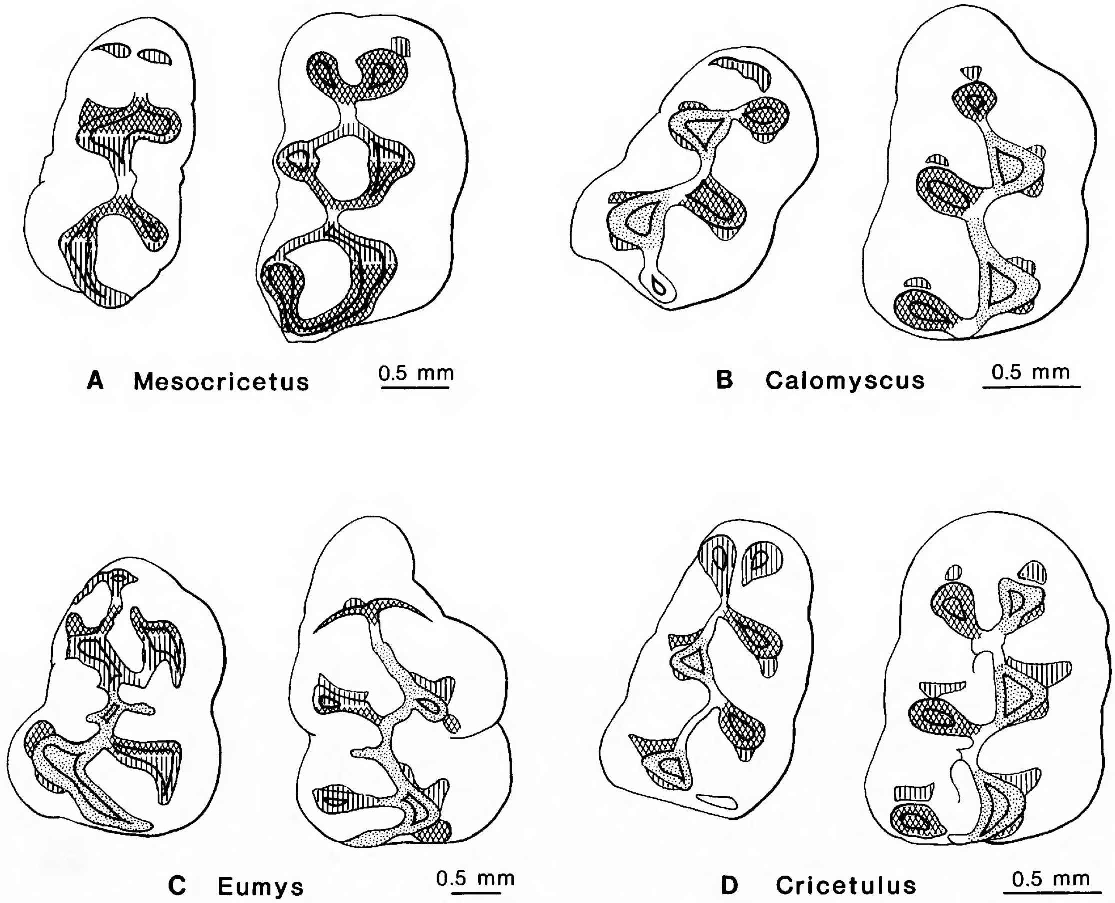

FIG. 3. First lower left and upper right molars of some cricetid rodents: A, *Mesocricetus auratus* (AMNH 144771); B, *Calomyscus bailwardi* (AMNH 88839); C, *Eumys elegans* (lower, F:AM 113190; upper, F:AM 103376); D, *Cricetulus barabensis* (AMNH 57896). Orientation and patterns as in Fig. 2; stippling indicates terraces.

transverse lophs that restrict movement during chewing. Fossettes become enclosed by wear in all lophs of the upper molars; fossettids form in both the metalophid and hypolophid of M_3 and sometimes occur in the metalophid of M_2. The endoloph and ectolophid are straight and parallel to the axis of the tooth row. The lingual part of the anterior cingulum on M^2 is not so prominent as in *Lophiomys* and is much smaller than in *Cricetops.* The anterocones and anteroconids are paired in both genera. In *Mesocricetus* M^2_2 and M^3_3 are proportionally narrower and longer than in the other taxa.

In *Calomyscus* (fig. 3B) the chief cusps do not form transverse lophs. The strong endoloph and ectolophid zigzag from one cusp to the next across each tooth. The chief cusps are obliquely opposite in M^2_2 and are alternate in M^1_1. The lingual and buccal embayments are alternate in M^1_1 and M_2. The third molars are very small and the crown pattern is unclear. The anterior cingulum has a single cusp in M^1_1. The posterior cingulum is lacking in upper molars. There is no enclosure of fossettes or fossettids. The teeth of *Calomyscus* are terraced by wear, a condition described by Hershkovitz (1962). Buccal cusps are higher than lingual in worn upper teeth and lingual higher than buccal in lower teeth. When the teeth are occluded manually, the high lingual cusps of the lower teeth can pass

smoothly between the high buccal cusps of the uppers and continue into the broad embayments between their low lingual cusps. At this point the lower teeth can be slid anterolingually across the uppers. The result of this motion is that buccal cusps of the lower teeth cross lingual cusps of the upper; both are worn apically, and this produces the terraces.

The teeth of *Eumys* (fig. 3C) are similar to those of *Calomyscus*: there is a single anterocone, -id in M^1_1; the endoloph and ectolophid have curved courses; with wear the teeth acquire terraced form. The chief differences are: buccal and lingual cusps and embayments are opposite; the lingual embayments in upper molars hook anteriorly around the buccal sides of the protocones; buccal embayments on lower molars are broad and weakly divided at the head by a small mesostylid; mesolophs are usually present in M^1 and M^2, and occasionally there is a mesolophid in M^1_1; posterior protolophules occur in M^2 and M^3 of some specimens (e.g., F:AM 94917) and with wear these enclose fossettes; a long posterior arm from the protoconid, the protolophulid, extends almost to the lingual side of the lower teeth; M^3_3 are relatively large teeth; the posterior cingulum is well developed in upper molars.

The teeth of *Phodopus* and *Cricetulus* (fig. 3D) resemble those of *Lophiomys, Cricetops, Cricetus,* and *Mesocricetus* in having opposite cusps and embayments in the upper teeth; the oblique crests and valleys are emphasized in the lower molars by wear. In *Phodopus* and some specimens of *Cricetulus* the endoloph is straight and longitudinal, whereas in other *Cricetulus* (AMNH 57722 and 57723) it is more obliquely oriented. The teeth are terraced; the worn surface of the terrace stands at an angle and obliquely faces the central axis of the tooth rather than being nearly horizontal as in *Eumys* and *Calomyscus.* Manual occlusion and evidence of wear facets indicate an initial lingual direction of the lower molars followed by an anterolingual motion that produced the series of terraces. The inclined orientation of the opposing terraces would have given the jaw a ventral component of motion during this phase of occlusion. Wear on the lingual side of upper teeth and buccal side of lowers in some specimens appears to have been made by the high cusps on opposing teeth and is consistent with such a propalinal phase of occlusion. Fossettes and fossettids are very narrow and disappear early in wear, especially in *Phodopus*; they are commonly formed in the upper molars and sometimes occur in M_3 but not in M_1 and M_2. The anterocone is always paired, the anteroconid, usually.

The percentage of the tooth row occupied by individual teeth and the proportions of these teeth are given in tables 2 and 3. In the upper dentition M^1 is the longest tooth and occupies an average of about 45 percent of the tooth row; distinctly higher percentages occur in *Lophiomys* and *Calomyscus.* The low ratio of width to length in M^1 indicates its rectangular shape. M^2 is the most uniform tooth in the series; usually it occupies slightly less than one-third of the tooth row and approaches a square shape, as a ratio close to 100 indicates. *Mesocricetus* diverges from the pattern with an elongated M^2. M^3 is large in *Cricetops, Cricetus,* and *Mesocricetus*; it appears elongated in the latter genus. In *Cricetops, Cricetus, Cricetulus,* and *Phodopus* it is approximately round. In *Eumys* and *Calomyscus* M^3 is shorter than wide. The percentage of the tooth row occupied by M^3 in *Calomyscus* is very low. In general, M^2 is the widest tooth or is equal in width to M^1; in *Lophiomys* M^1 is usually the widest tooth. M^3 is narrower than M^2 except in *Mesocricetus*; it is considerably narrower in *Lophiomys* and *Calomyscus.*

In the lower dentition the teeth are more alike in length than in the upper. The molars of *Eumys* each occupy about one-third of the total tooth row. In *Cricetops, Cricetus,* and *Mesocricetus* M_1 is about 36 percent of the total; in *Lophiomys, Cricetulus,* and *Phodopus,* about 40 percent; in *Calomyscus,* 43 percent. M_1 is clearly rectangular. M_2 and M_3 each occupy about 31 percent of tooth row length. Exceptions are a larger M_2 and much smaller M_3 in *Calomyscus* and the elongated M_3 in *Mesocricetus.* M_2 is more nearly equidimensional than either M_1 or M_3 with the exception of the round M_3 in *Calomyscus.* M^2 is usually the widest tooth but is not much different from M_1 and M_3 except in *Calomyscus* where M_3 is small. In *Lophiomys* M_1

TABLE 2
Relative Tooth Length

	Percentage of Upper Tooth Row Occupied by			Percentage of Lower Tooth Row Occupied by			
	M^1	M^2	M^3	M_1	M_2	M_3	N
Cricetops	45	29	26	36	32	32	13
Lophiomys	47	30	23	41	31	28	12
Cricetus	41	32	27	36	31	32	7
Mesocricetus	42	31	27	35	31	34	10
Cricetulus	45	31	24	39	30	30	10
Phodopus	45	30	25	40	31	29	10
Calomyscus	49	33	17	43	35	21	10
Eumys	45	31	24	34	32	33	12

TABLE 3
Tooth Proportions: Width/Length × 100

	M^1	M^2	M^3	M_1	M_2	M_3	N
Cricetops	62	95	98	70	85	85	13
Lophiomys	59	91	89	58	82	82	12
Cricetus	64	91	100	62	85	81	7
Mesocricetus	58	80	92	59	75	72	10
Cricetulus	64	95	102	63	88	82	10
Phodopus	65	94	99	64	89	84	10
Calomyscus	64	93	122	70	90	101	10
Eumys	66	98	118	79	90	86	12

is always the widest tooth by a slight margin. In some specimens of *Mesocricetus* M_3 is a little wider than M_2.

DISCUSSION

The chief problem encountered in assessing relationships within a group as ancient and diverse as the Cricetidae is distinguishing primitive and derived character states. Parallelism in the masticatory system is common in rodents, and other characters must be considered along with it to identify the different origins of derived states.

The condition in which buccal cusps are opposite lingual cusps appears to be primitive for the Myomorpha. It can be seen in the lower molars of *Microparamys* (Dawson, 1974); both cusps and bays are opposite in upper and lower molars of *Sciuravus* (Troxell, 1923), geomyoids (Rensberger, 1973), and many of the extinct eumyine and cricetodontine rodents. Lindsay (1972, p. 75) referred to alternation of cusps in the Miocene genus *Copemys* as a derived condition. Carleton (1980) proposed that opposite cusps are primitive for muroids.

The terraced teeth in *Eumys* and *Calomyscus* are probably primitive; this horizontal surface and a similar pattern of wear facets occur in extinct paramyid and sciuravid rodents. Restriction of occlusal motion to a transverse direction and the simpler wear facets found in *Cricetops, Lophiomys, Cricetus,* and *Mesocricetus* are derived and are rare among rodents. *Cricetulus* and *Phodopus* appear to be intermediate. Vorontsov (1979, p. 40) pointed out that the arc described by M_3 is less than that of M_1 in chewing; presumably the jaw joint functions as a pivot in this system. A consequence of the different arc lengths is that M^1 should be the widest part of the dentition. This is true only in *Lophiomys.* In all the taxa examined, however, the greatest width is anterior to M^3.

The endoloph and ectolophid are present in each taxon. The oblique courses seen in *Eumys* and *Calomyscus* are deemed primitive. A straight, longitudinal course, thinness, and early reduction by wear are almost certainly derived characters; these are developed best in *Cricetus, Mesocricetus,* and *Lophiomys.* The presence of mesoloph and mesolophid is common among the earliest known cricetids and is considered primitive (Hershkovitz, 1962); traces of these structures are found in *Cricetops*; they are better developed in *Eumys.* Enclosure of fossettes is a common derived character in upper molars of *Cricetulus, Phodopus, Cricetus, Mesocricetus, Cricetops,* and *Lophiomys.* Enclosure of fossetids in M_1 occurs only in *Cricetops* and *Lophiomys.*

Eumys is the most primitive rodent in this assemblage with regard to presence of mesoloph and mesolophid and terraced wear. Its short, broad M^3 is derived. *Calomyscus* is advanced in having extremely small M^3_3, no mesolophs and mesolophids, and alternating cusps in M^1_1.

Transverse wear is prominent in *Cricetulus* and *Phodopus,* but a tilted terrace is present. *Cricetus* and *Mesocricetus* are more special-

ized for transverse chewing. This group of four genera, the subfamily Cricetinae, is characterized by other specializations. All have large cheek pouches and a short tail that is less than 45 percent of head and body length.

Cricetops does not fit into this assemblage. Despite its hamster-like dentition, the skull lacks a zygomatic plate; the anteroventral part of the zygomatic arch remains as in protrogomorphous rodents and is primitive compared with the degrees of myomorphy seen in all the other taxa examined. The tail is unknown in *Cricetops.*

Cricetops, as described by Lindsay (1977) and restored by Vorontsov (1982, fig. 59), was hystricomorphous; rostral fibers of the anterior part of the medial masseter extended through the infraorbital foramen and arose on the side of the rostrum. This condition is considered to be the first step in the development of myomorphy by Klingener (1964) and Lindsay (1977). In fully myomorphous rodents, such as *Lophiomys* and the cricetines, the origin of the lateral masseter extends anterodorsally onto a zygomatic plate or alongside the infraorbital foramen, and the superficial masseter arises on the side of the rostrum. Wood (1965) has described the tendency in rodent evolution and the advantages of anterior shift of parts of the masseter. The expanded origin of the lateral masseter in myomorphs is analogous to the similar condition in sciuromorphous rodents. Among these, the modification is known to have occurred independently in at least three lineages, the Ischyromyidae, Sciuridae, and Geomorpha; the Castoridae may represent a fourth instance. Given the advantage of this modification and its multiple origin, it is likely that the same change may have arisen several times among the earliest, hystricomorphous members of the Myomorpha.

Lophiomys is unusual in having an expanded skull roof, reduced clavicles, and complex stomach. These are derived characters that would not bar its sharing close relationship with *Cricetus* and *Mesocricetus.* But, since cheek pouches have not been reported in *Lophiomys,* and its tail averages 62 percent (six specimens) of head and body length, the genus cannot be derived in common with any of the living cricetines. The similarity of dental design is a likely example of parallelism.

The dentitions of *Cricetops* and *Lophiomys* are so similar that close relationship between the two genera is possible. Enclosure of fossettids in M_1 is a unique, derived character that they share in addition to transverse ridges and wear; the character does not occur in living cricetines. Vorontsov (1979, p. 31) described specialized features and noted that "in *Cricetops* (aff) *affinis* thick zygomatic arches are highly developed . . . ." The jugal portion of the zygomatic arch in *Cricetops dormitor* (AMNH 19051) is much broader dorsoventrally than that of the cricetines or *Calomyscus.* The jugal is also broad in *Eumys* (AMNH 94108) and *Paramys,* and thus a broad jugal appears to be primitive. The jugal is broader in *Cricetops* than in these rodents; this broadening may be a derived character expressed by extreme expansion in *Lophiomys.*

Since emphasis on the transverse component of chewing is shared by *Cricetops, Lophiomys,* and the Cricetinae, these taxa may share common ancestry as suggested by Schaub (1925). *Cricetops* and *Lophiomys* can be included in a single subfamily, the Lophiomyinae, suggesting that the myomorphous condition of the masseter was invented in parallel with that of the Cricetinae and of other cricetid taxa. The greater development and anterior extent of M_1^1 in *Lophiomys* can be derived from the conditions seen in *Cricetops.*

CONCLUSIONS

A cladogram (fig. 4) illustrates the hypothesized relationships between *Cricetops, Lophiomys* and the cricetine genera. Derived features that define numbered nodes are:

1. Muroid cheek tooth formula of M_{1-3}^{1-3}; tooth shape rectangular with crown pattern and based primitively on five crests; rostral fibers of medial masseter penetrating infraorbital foramen.
2. Transverse component of occlusion emphasized and terraced surfaces in molars reduced; lingual-buccal cusp pairs forming transverse crests; fossettes enclosed in

upper molars; mesolophs, -ids reduced; anterocones paired in M^1.
3. Transverse crests of molars strong and terraces absent; fossettids enclosed in M_1; jugal bone dorsoventrally wide.
4. Buccal cusps of upper teeth rotated and abrupt edge formed with posterior wear surfaces.
5. Expanded cranial vault; fully myomorphous masseter; M^1 longest, widest tooth; M^3 reduced; anteroconid paired in M_1; mesolophs, -ids absent; clavicles reduced; stomach specialized.
6. Fully myomorphous masseter; molar terraces tilted; anteroconid usually paired in M_1; mesolophs, -ids absent; cheek pouches present; tail short relative to head and body length.
7. Transverse crests of molars strong and terraces absent; anteroconid paired in M_1.

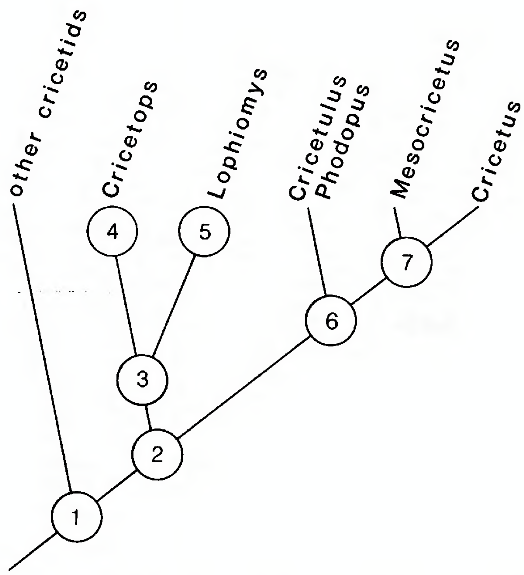

FIG. 4. Cladogram of proposed relationships between *Cricetops, Lophiomys,* and cricetine genera. *Calomyscus* and *Eumys* are included with other cricetids. For a list of derived characters defining nodes, see numbered section of Conclusions.

The proposed phylogeny is consistent with the following classification:

Family Cricetidae Murray, 1866
  Subfamily Lophiomyinae Milne Edwards, 1867
    Cricetops
    Lophiomys
  Subfamily Cricetinae Murray, 1866
    Cricetulus
    Phodopus
    Mesocricetus
    Cricetus
  other cricetid subfamilies

The family name Lophiomyinae takes precedence over the taxon Cricetopinae, which was created later. The name Lophiomyinae is here attributed to Milne Edwards (1867b, p. 114), who stated, "*Je proposerai donc d'établir à côté de la famille des Murides, et sous le nom* LOPHIOMIDES, *une nouvelle division du même rang* . . . ."

The proposed phylogeny is geographically plausible. The subfamily Cricetinae, especially the most primitive genera *Cricetulus* and *Phodopus,* is chiefly a northern Asiatic group. *Cricetops* is known from the center of the region. The cricetines inhabit open grasslands and dry, rocky environments. *Lophiomys* is arboreal, but it is found in woodlands on drier mountain massifs and in rocky areas (Kingdon, 1974). If *Lophiomys* is closely related to *Cricetops* and the Cricetinae, its ancestors must have come from Asia to Africa. Paleogeographic evidence (Smith, Hurley, and Briden, 1981) suggests that entry may have occurred in the late Miocene or later time via the Middle East. Relatives of *Lophiomys* should not be present among the earlier Miocene cricetids described by Lavocat (1973) from eastern Africa. Since the nature of tooth wear cannot be assessed from photographs or most casts, I have not been able to carry out this test of the proposed phylogeny. Other representatives of the Lophiomyinae may occur in Asia, but until now *Lophiomys* has not been an obvious choice for comparison with fossil cricetids.

Had myomorphy been considered to indicate common ancestry of *Lophiomys* and the cricetines, then *Lophiomys* would have diverged between nodes 2 and 6 in the cladogram. The hypothesized monophyly of *Cricetops* and these taxa would still stand.

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